A REVIEW OF LITERATURE ON MENHADEN WITH SPECIAL REFERENCE TO THE GULF OF MEXICO MENHADEN



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A REVIEW OF LITERATURE ON MENHADEN WITH SPECIAL REFERENCE TO THE GULF OF MEXICO MENHADEN, Brevoortia Patronus GOODE

by

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ABSTRACT

Menhaden have been important commercial fishes in the United States since colonial days. In this review of the literature on menhaden biology, scattered sources of information are brought together. The chief papers on Atlantic menhaden and practically every piece of biological literature on Gulf of Mexico menhaden are cited. Atlantic and Gulf menhaden literature are treated separately in topical arrangement.

The menhaden fishery developed sporadically in the Gulf of Mexico until 1939. Landings exceeded 200 million pounds for the first time in 1949 and the record catch of 1956 was more than 550 million pounds. Most of the Gulf landings come from Louisiana waters.

There are five North American species of Brevoortia. B. smithi inhabits both Atlantic and Gulf waters. The Atlantic menhaden fishery is dependent on B. tyrannus and Gulf menhaden fishermen catch B. patronus.

Brevoortia tyrannus spawn at sea, or in high salinities, and the larvae move to low salinity areas which are essential to their development. Spawning time apparently depends on water temperature and occurs off the South Atlantic States in winter and in spring and summer farther north. Menhaden eggs and early larvae have not been reported from the Gulf of Mexico. Collections of larvae and juveniles indicate that Brevoortia patronus spawn in high salinities during the fall, winter and spring.

Larvae reach low salinity waters before metamorphosis. On the nursery grounds, body proportions change from the larval stage to the adult at about 30 mm. standard length, and the young fish move toward open waters of higher salinity in the summer and fall. The number of young on the nursery grounds varies greatly from year to year. No long migrations of menhaden are known in the Gulf. There are little data on the growth rate of Gulf menhaden.

Brevoortia patronus is known to feed by filtration and, in turbid estuarine waters, consumes considerable quantities of detritus and suspended bacteria in addition to living plankton.

Bluefish, mackerel, sharks and tarpon are the chief enemies of Gulf menhaden, and birds take a toll. The common shore and shallow-water sport fishes seem not to subsist to any great extent on larger menhaden, but predation upon small menhaden in the bays seem to be heavy. A few menhaden have been reported killed in the Gulf by sudden cold waves and the "red tide" kills numbers of menhaden in Florida waters.

There is no evidence that menhaden are affected by any fatal diseases in the Gulf of Mexico but they are characteristically host to a number of worm and crustacean parasites.

Few fish other than menhaden are taken by menhaden fishermen.

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INTRODUCTION

On the Atlantic coast of the United States, menhaden have been utilized for food and for fertilizer since the days of the early colonists (Goode, 1879). Processing the fish for oil, which in the beginning consisted merely of pressing the decomposing raw fish, was started in Rhode Island in 1811 (Goode, 1884). In the 1870's the industry was brought to North Carolina by northern soldiers who had noted the abundance of menhaden in southern waters during the Civil War (Ellison, 1951). After some initial failures the menhaden industry became well established in the South Atlantic States in the 1880's.

Despite the long history of the menhaden fishery in the Atlantic and its rapid expansion in the Gulf of Mexico, extensive studies of the biology of these important commercial fishes have not been undertaken until recently. The only published bibliography on biology of the American Menhaden (Reintjes, Christmas, and Collins, 1960) includes most of the literature with very brief annotations and a subject index. This review of the literature on the biology of menhaden brings together information from somewhat scattered sources. Gulf commercial production is discussed first, followed by a summary of the taxonomy, distribution and relationships of the species of the genus Brevoortia. The Atlantic menhaden, Brevoortia tyrannus (Latrobe), is discussed under topic headings. The chief papers are cited, but no attempt was made to cover completely the voluminous and sometimes repetitious literature. In the section on the Gulf menhaden almost every piece of literature pertaining to the biology of this species has been cited. Topical arrangement of the material parallels that of the Atlantic menhaden.

GULF MENHADEN FISHERY STATISTICS

The development of a menhaden fishery in the Gulf States moved from east to west. There was considerable production of menhaden on the Florida east coast as early as 1923 but continuous production did not start in the Gulf States until 1937 (Power, 1958). The production statistics shown in table 1 were taken from various U.S. Fish and Wildlife Service reports. There are some State statistical reports, but these are not comparable from State to State nor from year to year. They would be of little value except for the years 1946-47 in the developmental period of the Gulf menhaden fishery.

Catch records given by Anderson and Peterson (1953) show that menhaden were caught off the west Florida

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coast as early as 1880. From 1902 to 1938 annual production in this area fluctuated between 2,000 and 18,815,000 pounds and the annual average was 7,059,000 pounds for the 13 years reported. Alabama reported 10,000 pounds in 1902 and 4,000 pounds in 1931. Texas reported 14,118,000 in 1918 and 8,517,000 pounds in 1923. No other menhaden catches from the Gulf of Mexico were reported during the years 1880 to 1938. Therefore, it may

be said that the Gulf menhaden fishery got started in 1939 with the location of plants in Mississippi.

During the World War II years Gulf production came from Florida and Mississippi. By 1948 plants had been located in Louisiana and Texas. Landings did not exceed 200 million pounds until 1949.

Table 2 shows the total catch, yearly average and percentage catch

Table 1.--Landings of Gulf of Mexico menhaden by States, 1939-58

[In thousands of pounds]

Year	West coast Florida	Alabama	Mississippi	Louisiana	Texas	Total Gulf	Source
1939	2,849	O	9,000	O.	0	11,849	Anderson & Peterson (1953)
1940 1941 - 44		0	25,195 (No data	0 collected)	0	25,462	Fiedler (1943)
1945	7,106	Ō	57,340	C	0	64,500	Anderson & Fower (1949)
1946-47			(No data	a collected)			
1948	'No data collected)	68,631	<i>\$8,</i> 110	28,185	184,931	Anderson & Power (1951)
1949		0	44,579	105,913	41,136	276,507	Anderson &
1950	1,534	0	69,550	207,755	47,191	326,030	Feterson (1952) Anderson & Peterson (1953)
1951	3,375	0	114,895	209,574	30,121	357,965	Anderson &
1952	10,737	0	112,890	283,373	52,984	459,984	Peterson (1954) Anderson & Power (1955)
1953	4,031	0	58,933	307,492	66,589	437,045	Anderson & Power (1956a)
1954	2	0	79,445	270,094	51,702	401,243	Anderson & Power (1956b)
1955	1,935	0	128,123	298,309	52,625	÷30,992	Anderson & Power (1957)
1956 1957 1958	7	0 0 0	172,592 142,124 123,346	320,521 162,817 241,813	66,691 57,585 68,559	559,836 362,533 442,826	Power (1958) Power (1959) C.F.S. No. 2165

Table 2.--Menhaden landings of the Gulf States, 1949-58

[In thousands of pounds]

Location	Totals	Yearly average	Percent
West Florida	55,640	5,564	1.4
Alabama	0	0	0
Mississippi	1,046,477	104,648	25.5
Louisiana	2,467,661	246,766	60.1
Texas	535,183	53,518	13.0
Total	4,104,961	440,496	100.0

by Gulf States for the years 1949-58, inclusive. The Florida catch was negligible, being slightly more than I percent of the total. No menhaden landings were reported from Alabama. The major part of the catch, over 60 percent, was landed in Louisiana. However, table 2 does not fully show the preponderance of Louisiana waters in menhaden production. Statistics are not available on catch localities, but Texas boats have little Texas water in which to fish (Baker, 1955) and the Mississippi coast line is less than 70 miles long.

In 1950 the Gulf catch was 32.6 percent of the United States total (table 3). In 1955, although the Gulf catch had increased to over 480 million pounds, the Gulf percentage of the United States total catch declined to 25.8. Gulf fishermen took 26.7 percent of the record catch of 1956, when over 2 billion pounds were reported for the United States total landings. Total landings dropped sharply in 1957. Power (1959) listed several reasons for the 1957 decrease. Although the number of purse seines (table 4) continued to increase in the Gulf, the 1957 Gulf catch was down to 21.5 percent of total landings.

Little information on catch per unit effort is available in the Gulf menhaden fishery and the period of time during which the fishery has operated at a high level is only 10 years. While the number of yards of seine (table 4) for the Gulf coast men-

haden fishery more than doubled from 1948 to 1958, the catch per yard increased from 13.9 thousand pounds to 19.8 thousand pounds in 1956. The catch per yard of seine dropped to 11.6 thousand pounds in 1957 and came back to 13.9 thousand pounds in 1958.

MENHADEN BIOLOGY

TAXONOMY, DISTRIBUTION AND RELATIONSHIPS

Menhaden belong to a genus of clupeid fishes inhabiting the shore regions of the Atlantic from Nova Scotia to Argentina and, according to de Buen (1958), Pacific waters off Chile and Peru. Unverified records place the genus off the west coast of Africa.

The genus Brevoortia was established by Gill (1861). Brevoortia tyrannus (Latrobe) was designated the genotype. The genus was revised by Goode (1878) and by Hildebrand (1948). According to Hildebrand (1948) there were seven species, five in North America and two in South America. Hildebrand had no North American records south of Indian River, the coastal lagoon of east Florida, and none south of Tampa on the west Florida coast. The mouth of the Rio Grande River was the southern limit in the western Gulf. Hildebrand was quite firm in asserting, as a result of his sojourn in Dry Tortugas, that there were no menhaden in southern Florida.

Table 3.--Total landings of Atlantic and Gulf of Mexico menhaden, 1950-57

[In thousands of pounds]

Year	Atlantic	Gulf	Totals
1950	. 674,468	326,030	1,000,498
1951		357,965	1,103,915
1952	,	459,984	1,383,590
1953	,	437,045	1,696,076
1954	-	401,243	1,737,767
1955	. 1,386,791	480,992	1,867,783
1956		559 , 836	2,097,239
1957		362,533	1,690,128

Table 4.--Number of purse seines, number of yards of seine, and catch per yard of seine for the Gulf coast for various years

Year	Number of purse seines	Number of yards of seine	Catch per yard in thousands of pounds	Source
1948	34	13,350	13.9	Anderson & Power (1951)
1949	53	20,125	13.7	Anderson & Peterson (1952)
1950	66	24,600	13.3	Anderson & Peterson (1953)
1951	64	24,300	14.8	Anderson & Power (1954)
1952	71	27,000	17.0	Anderson & Power (1955)
1953	74	28,575	15.3	Anderson & Power (1956a)
1954	63	23,502	17.1	Anderson & Power (1956b)
1955	67	26,019	18.5	Anderson & Power (1957)
1956 1957 1958	75 79 80	28,225 31,171 31,949	19.8 11.6 13.9	Power (1958) Power (1959) C.F.S. No. 2165

No members of this genus had been reported from South America north of Salvadore (Baia), Brazil or from the West Indies.

One exception to the generally accepted western Atlantic distribution of Brevoortia is the statement of Goode (1879) concerning a menhaden in the eastern Atlantic. He said large schools of B. dorsalis of West Africa had been reported to him. Fowler (1936) synonymized the African menhaden with B. tyrannus. Since no specimen was available for check, Hildebrand (1948) doubted the identification. Briggs (1958) listed B. tyrannus from Africa, but gave no records.

De Buen (1958) reduced the genus Ethmedium (Thompson, 1916) to subgeneric status in the genus Brevoortia, thereby extending the range of Brevoortia to the Pacific coasts of Peru and Chile. De Buen's arrangement places the seven species of Brevoortia recognized by Hildebrand (1948) in a subgenus, Brevoortia, and

adds Brevoortia (Ethmidium) maculata (Valenciennes) 1847 and Brevoortia (Ethmidium) chilcae (Hildebrand) 1946 to the genus Brevoortia.

Brevoortia tyrannus of the Atlantic is the most important and abundant menhaden known (Ellison, 1951), and approximately 73 percent (table 3) of all the menhaden landed in the United States from 1950 to 1957 belonged to this species. The Atlantic menhaden has been reported from the Bay of Fundy to Indian River, Florida, and has been fished from Maine to Mayport, Florida.

Goode (1878) described Brevoortia patronus from specimens collected in the Gulf of Mexico at Brazos Santiago, Texas. Jordan and Evermann (1896) listed the Gulf menhaden as Brevoortia tyrannus patronus Goode. Regan (1917) placed Brevoortia patronus in synonymy with B. tyrannus. Gunter (1945) stated that "Brevoortia patronus Goode, as some authors would have it", had been recognized as the only species of

menhaden in the Gulf. Since only specific names were used in his paper, Gunter (1945) referred to B. t. patronus as B. tyrannus. Hildebrand (1948) also noted that B. patronus had generally been considered by authors as only subspecifically distinct from B. tyrannus or identical with it. However, Hildebrand's diagnosis showed that B. patronus had fewer oblique scales, fewer modified scales in front of the dorsal, fewer vertebrae, fewer ventral scutes and fewer pectoral and dorsal, and more anal rays. The lower caudal, pectoral, maxillary and lower mandible were generally longer. The head was longer and deeper and body depth was greater. B. patronus was accorded full specific rank in Hildebrand's 1948 revision of Brevoortia. Meristic characters indicated that B. patronus resembled B. tyrannus of eastern Florida more than it did B. tyranius farther north. Hildebrand (1948) noted that the lack of a decrease in number of vertebrae in southern menhaden was contrary to the general observation of lower vertebrae counts for other fishes in warmer waters.

Hildebrand (1941) described a small-scaled, nonslimy, yellow-finned menhaden from the coast of Carolina and named it smithi. He had previously (Hildebrand, 1920) called this fish Brevoortia aurea (Agassiz), which is a South American species. The range was given as Beaufort, North Carolina, to Indian River, Florida. Hildebrand (1941) noted that B. smithi was not abundant, did not school in large numbers, and was called "yellowfin shad" by local fishermen. He said the fishermen kept fish of this species aside and carried them home for food. Suttkus (1958) reported B_{\bullet} smithi from the eastern Gulf of Mexico between Cedar Keys and Placida, Florida, noting "... that Hildebrand was aware of the presence of Brevoortia smithi in the Gulf of Mexico long before I made my independent discovery."

Gunter (1945) noted a second species of menhaden in the Gulf which he said was close to if not identical with *Brevoortia smithi* of the Atlantic. Hildebrand (1948) described this as a

new species, B. gunteri, which he considered to be a Gulf cognate of B_{\bullet} smithi. B. smithi and B. gunteri agreed in having small scales, pointed yellowish fins, more silvery color and less green along the back, and in being notably less slimy than B. tyrannus and B. patronus. B. gunteri differed from B. smithi in having a larger head, greater depth and longer maxillaries, mandibles and pectorals. The ventral scutes and vertebrae were fewer in number. Hildebrand (1948) examined specimens from Grand Isle, Louisiana; Aransas Bay, Texas; and the mouth of the Rio Grande, Texas.

The fifth North American species of *Brevoortia* is *brevicaudata*. Goode (1878) described the species from the only known specimens, collected at Noank, Connecticut, in 1874. Hildebrand (1948), after re-examining these specimens, listed nine ways, including the short caudal fin, in which they differed from *B*, tyramus. Scalation was similar to that of *B*, tyramus. Bigelow and Schroeder (1953) questioned the correctness of these views.

The ranges of *Brevoortia aurea* (Agassiz) and *Brevoortia pectinata* Jenyns in South America are not well known.

Hildebrand (1948) pointed out that the seven American menhaden could be divided into a large-scaled group, B. tyraunus, B. brevicaudata, B. patronus, B, pectinata, and B, aurea, and a smallscaled group, B. smithi and B. gunteri. He further stated that these menhaden could also be divided into two groups according to the shapes of the ventral fins. Brevoortia tyrannus, B. brevicaudata, and B. patronus had rounded fins, while the other four had pointed fins. The two South American species differed from the others by less reduction in size of the scales on the back and on the base of the caudal as compared to mid-scales on the sides.

Hildebrand (1948) noted that with the exception of B_{\bullet} brevicaudata, North American species of Brevoortia could be divided into two closely related pairs on either side of the Florida

peninsula. Species of sciaenids and clupeids, which are cognate on the east and west sides of Florida, were listed to support Hildebrand's theory that the paired species of menhaden differentiated after the peninsula last rose above the sea.

ATLANTIC MENHADEN

Spawning

Peck (1894) said minute organisms furnish food for menhaden "not only within the limits of these brackishwater inlets and estuaries where the spawn is left to develop" but also in more open waters, apparently having come to this conclusion concerning spawning because small fish were abundant in estuarine situations around Woods Hole, Massachusetts, in the summer of 1893. Peck also pointed out that low salinity areas were important "because they were intrusted with so much embryonic and larvallife of the migratory inhabitants of the coast." Smith (1907) said that in New England the spawning of menhaden took place in late spring and early summer, and from Chesapeake Bay southward spawning occurred in late fall and early winter. Fishermen reported large fish with full roe in November and December in North Carolina "rivers", but disagreed as to whether the spawning act took place only in the ocean (Smith, 1907). Schools of young were found inshore in winter. However, Smith was not sure of the spawning location and said "there is some evidence" that spawning took place both in the sea and inside waters.

Kuntz and Radcliffe (1918) found some fish ready to spawn and some spent in Woods Hole harbor in August. Eggs and larvae were occasionally taken there during the summer and were abundant off Gay Head in August. Larvae 20 mm. long were taken in the harbor on October 21, 1914. These authors indicated that the main spawning period in the Woods Hole area was June, July, August, "and later".

Bigelow and Welsh (1925) found spent and ripe fish in the Gulf of Maine

in July and August. They said spawning around Woods Hole took place from June to October. The *Grampus* (Bigelow and Welsh, 1925) took eggs and larvae in Nantucket Sound and west of Martha's Vineyard in October 1915. Bigelow and Schroeder (1953) reported no eggs and larvae north of Cape Cod but said fry were taken in abundance in Casco Bay in 1900.

Warfel and Merriman (1944) found menhaden larvae (less than 23 mm., standard length) in the harbor of New Haven, Connecticut, in July and September. The standard length of menhaden collected in October was 30 mm. and a few 38-55 mm. in standard length remained until November.

Perlmutter (1939) reported eggs and larvae at 27 of 52 stations in Long Island Sound. He said the spawning season extended from May to October. Westman and Nigrelli (1955) said menhaden in the zero year class appeared in estuaries, tidal rivers, creeks, mooring basins and canals in June 1953 and remained until late September or October. Eggs and larvae were not found in Great South Bay by Perlmutter (1939) although zeros (young-of-theyear) more than an inch in length were usually abundant there inshore. According to Westman and Nigrelli (1955) "The abundance of these young menhaden is difficult to imagine and, unlike the adult population they exhibit no aversion to fresh water." Due to the long spawning season some of the young-of-the-year were 7 inches long in October and others were only 2 inches long. Evidently Westman and Nigrelli did not collect larval stages.

Radcliffe (Kuntz and Radcliffe, 1918) took larvae 30 mm. long at the mouth of the Potomac in February 1914. According to Hildebrand and Schroeder (1928), menhaden in the Chesapeake Bay region seemed to spawn in the fall. Larvae averaged 27.7 mm. long in January, 33.5 mm. in February, 27.3 mm. in March, 33.0 mm. in April, and 46.0 mm. in May. Pearson (1950) took menhaden larvae at Old Point Comfort, Virginia, during April and May.

Massman, Ladd and McCutcheon (1954) caught young menhaden in the brackish and fresh waters of four Virginia Rivers, up to 27 miles above brackish waters, in April and May. These fish were collected in plankton tows and ranged from 24 to 30 mm. standard length. Ninty-eight percent of the 8,000 specimens were found at salinities of 2-3 ‰. The ratio of numbers caught in surface and bottom tows was 200 to 1. In June, menhaden of 40.6 mm. in mean standard length were the most abundant species in the shore zone just above brackish water. Young fish were present in July in the same area. Surface trawls showed essentially the same pattern in September when fish averaged 94 mm. standard length.

Ellison (1951) quoted Hardcastle (MS) who concluded that, in North Carolina, menhaden probably spawn in late winter near the Gulf stream. Ellison (1951) said the young fish have wide salinity tolerance and live in slightly brackish waters or waters with the salinity of sea water, and quoted Westman and Bidwell (1948) who reported young 45 miles up the Hudson River and in Long Island Sound at the same time.

Bigelow and Schroeder (1953) said that W. W. Welsh concluded that sexual maturity in menhaden is attained by the third year of life. Westman and Nigrelli (1955) wrote that all menhaden 3 years of age or more appeared to be adult fish.

Goode (1884) reported that 150,000 eggs were found in one menhaden.

Ellison (1951) quoted Hardcastle (MS) who found that 41 percent of mature and immature males were infested with a gonadal parasite, *Eimeria brevoortia*, a sporozoan. The effect of this infestation on sperm production was not determined.

Perlmutter (1939) is the only author who has reported salinities at which menhaden spawn. He gave the figure as 84-100 percent (30.5 - 35%) sea water, at 55°-80° F. All other re-

ports of menhaden eggs correspond with high salinity situations.

Growth

Kuntz and Radcliffe (1918) reported that menhaden eggs were 1.4-1.6 mm. in diameter. Bigelow and Schroeder (1953) gave the measurements as 1.5-1.8 mm. and said menhaden produced the largest fish eggs to be found in the Gulf of Maine.

McHugh, Oglesby and Pacheco (1959), after studying the Chesapeake Bay pound-net and purse-seine fisheries, assumed that, in the Chesapeake Bay area, menhaden left the Bay as they approached maturity in late September, October and November. Spawning apparently occurred outside the Bay in the fall and continued through the winter. Bimodal distribution of length and weight frequencies in agegroup 0 suggested that two spawning peaks may occur in the Chesapeake region.

Welsh (Bigelow and Welsh, 1925) found experimentally that hatching took place in less than 48 hours and that the larvae are 4.5 mm. long at that time. Four days after hatching they were 5.7 mm. long. There are no other data on the time element and growth of the larvae. The dorsal and caudal fins were visible in the 9 mm. stage and all fins were differentiated at the 23 mm. stage. At this stage the larva was long and slim; when the young menhaden had reached 33 mm. in length it had taken on a more fish-like appearance and acquired scales.

June and Chamberlin (1959) demonstrated that low salinities are essential to the normal development of Atlantic menhaden larvae. Larvae and metamorphosing individuals from low-salinity areas invariably perished when transplanted to high-salinity rearing ponds, although individuals transplanted a few weeks after metamorphosis survived. Similar phenomena were observed in natural conditions on several occasions. Larvae reared through

metamorphosis in high salinities developed abnormalities while those developing at low salinities were normal.

Hildebrand (1948) has noted that all species of young menhaden (aurea and smithi not verified) up to 70 mm. long have minute teeth on the margin of the maxillary which are subsequently lost.

Welsh (Bigelow and Welsh, 1925) studied large numbers of menhaden fry and their scales in the Gulf of Maine. Summer hatched fish were found to be 6-8 cm. long the first winter and 16 cm. long the second winter. Bigelow and Schroeder (1953) reported young menhaden 9.1-9.9 cm. long at Woods Hole in late September 1942. Fish taken at Falmouth, Massachusetts, 2 months later were 11.7-12.7 cm. long. Welsh (Bigelow and Welsh, 1925) found as many as nine to ten "winter rings" on the scales of a few of the older fish examined and apparently thought that each ring represented 1 year's growth.

Rush (1952) found that fish with one annulus at Beaufort, North Carolina, were approximately 18.9 cm.long (fork length). Three-year fish were 28.7cm. long. The oldest fish, 6 years, was 35.8 cm. long. The growth curve was worked out on 34 specimens. Westman and Nigrelli (1955), who worked on Long Island Sound fish, stated that growth rates determined "upon the basis of many times that number of specimens" were very similar. Fish showing a single annulus averaged 18.4 cm. fork length. Fifty-two males of age class III ranged from 29.5 to 34.0 cm. fork length and 52 females of the same age class ranged from 28.5 to 34.5 cm. long. In age class IV 17 males ranged from 31.5 to 35.0 cm. long and 55 females had a fork length range of 31.5 to 36.0 cm. They stated that the conversion factor from fork to total length was 1.1163. Scattergood, Trefethen and Coffin (1951) reported the conversion factor from standard to fork length to be 1.0459.

June and Roithmayr (1960) reported results of readings of 13,510 scale samples of Atlantic menhaden

taken along the east coast of the United States between Portland, Maine, and Fernandina, Florida, from 1952 through 1956. Scale formation commenced at body lengths between 24 and 30 mm., appearing first in the region of the caudal peduncle and later near the base of the pectoral fins and along the posterior margin of the opercles. Scales were fully formed at body lengths between 30 and 43 mm. Growth of scales of young-of-the-year was traced from May until mid-September. The first age ring was formed sometime after the first summer of life.

Ring formation occurred only once each year, between March and May. Marginal scale growth occurred during the warm months of the year. The distance between the last submarginal ring and the margin of the scale reached a maximum in the fall. The distance between the last two adjacent ring modes decreased with age. In general, ring formation was found to occur earliest in southern waters and progressively later farther northward. New varied considerably scale growth among individuals, especially in the younger age groups, and this variability is greatest in those fish occurring in southern coastal waters.

Hildebrand and Schroeder (1928) said that sexes could not be differentiated externally and that the growth rates were apparently much the same. However, Westman and Nigrelli (1955) analyzed the matter statistically and found that there was a significant difference, the females outgrowing the males.

Westman and Nigrelli gave fork-length frequency curves for 1/2-month periods from April to June for fish from Long Island Sound and New Jersey waters. In general, the curves showed a decreasing mode from about 30 cm. in April to 25 cm. in June during 1948 and 1949.

Ages of menhaden up to the third year of life may be determined by the length-frequency method or by reading scales (McHugh, Oglesby and Pacheco, 1959). Two groups of fish, characterized by their size at the time of formation of the first annulus, entered the Virginia fishery in 1954 and 1955 suggesting that growth rates differ according to circumstances. Mean lengths at the end of each calendar year of life were found to be approximately 125, 200 and 230 mm. Mean weights were about 30, 130 and 200 g. Menhaden reached maturity at about $l\frac{1}{2}$ years.

Hildebrand and Schroeder (1928) said that fish varied in fatness during the year and were much fatter in the fall than in spring. They also noted that fatness, and presumably growth rate varied from year to year. Fish, taken in October 1921, 13.0 cm. long averaged 0.78 oz. in weight, and two specimens of the same length, taken a year later, averaged 1.07 oz. In 1921, October fish 23.1 cm. long averaged 4.22 oz. and a similar sample for 1922 averaged 5.17 oz. The October 1922 fish weighed an average 15.5 percent more than fish of the same length taken October 1921. Hildebrand and Schroeder also gave some tables on weight-length relationships. Fish 10.2 cm. long weighed 0.35 oz., those 20.3 cm. long weighed 3.59 oz. and 35.6 cm. long weighed 17.1 oz.

Goode (1879) measured 30 fish from the same school taken at Noank, Connecticut, in 1875. They ranged from 12 to 13 inches in length and 10 to 16 ounces in weight. The average length was 12.38 inches.

Concerning seasonal changes in fatness, Bigelow and Schroeder (1953) said that menhaden were always thin when they arrived in the Gulf of Maine from the south, but put on fat rapidly. In 1894 the yield of oil rose from 12 gallons, and less, per thousand fish in the early part of the season to $14\frac{1}{2}$ in August to 16 and 18 gallons in September. They stated that New England fish were larger and fatter than those to the south. These authors also said that the longest menhaden of their knowledge was a specimen 18 inches long taken at Woods Hole in 1876, but that 29-inch fish had been reported. The heaviest fish reported was one from Orient,

New York, weighing 1 pound 13 ounces. Goode (1879) said the largest specimen in the National Museum was a 20-inch cast. These remarks do not correspond to those of Ellison (1951) concerning the abundance of 16- to 20-inch fish in North Carolina waters in late November.

June and Reintjes (1959 and 1960) presented extensive tables of length and weight frequency distributions of samples of Brevoortia tyrannus from the purse-seine and pound-net fisheries along the Atlantic coast from 1952 through 1956. Comparison of the average length and weight of individual year classes from the middle Atlantic area at different ages showed rather marked variation in fish of comparable age in the different years. The average fork length of age 1 fish ranged from 209 mm. in 1952 to 229 mm. in 1955; of age 2, from 233 mm. in 1952 to 259 mm. in 1955; of age 3, from 279 mm. in 1955 to 286 mm. in 1956; and of age 4, from 291 mm. in 1955 to 304 mm. in 1954. Five-year-old fish averaged 311 mm. fork length in 1956. The most striking feature was that in every year through 1955 fish of the dominant 1951 year class averaged lighter than adjacent year classes. In general, there was an increase in the size and weight of fish of the same age group from south to north. (It should be noted, however, that the fishery starts earlier in the south than it does farther north.) The data show that fish of the dominant year class which contributed to the catch in each area in 1956 were shorter and lighter than fish of the same age in 1955. Females were larger than males at older ages.

Distribution and Migrations

Bigelow and Schroeder (1953) reported that spawning probably took place every year from the Long Island Sound area to Florida during the period of their observations, and that in some years it extended into the Gulf of Maine. The eggs were buoyant, according to Welsh (Bigelow and Welsh, 1925) and were found at the surface in waters of high salinity (Perlmutter, 1939).

The larvae moved towards shore, where they reached sheltered and often low-salinity areas at a size of around 25 mm. standard length. Probably they were mostly at the surface during these movements. There were some indications that the larvae moved inshore shortly after coming into the estuaries and moved back out again as juveniles Ladd and McCutcheon, (Massman, 1954). Apparently this movement continued on out into open waters, for in December 2-inch fish, the zeros of Westman and Nigrelli (1955) showed up regularly in North Carolina mixed in with 10-inch fish (Ellison, 1951). Presumably the 2-inch fish came from the north, possibly Chesapeake Bay, because the North Carolina zeros should not be that size in December (Hildebrand, 1920).

McHugh, Oglesby and Pacheco (1959) found that menhaden less than 2 years old were present in Virginia waters throughout the year. Spawning probably took place in the ocean, and the young moved into Chesapeake Bay and its estuaries soon after hatching. As they grew, young menhaden moved back down the estuaries toward the sea. In most seasons mean sizes of fish were progressively greater in a seaward direction. Since the purseseine fishery exploited fish primarily in their second and third year of life and the pound-net fishery took principally fish in their first and second year, sampling of the pound-net fishery offered a method of forecasting purseseine catches at least a year in advance. Seasonal waves of emigration and immigration to Chesapeake Bay were associated with intense fall and spring periods. Females spawning slightly larger than males of the same age, but the difference was insignificant in young menhaden.

There is some information concerning the movements of *B. tyrannus* up and down the Atlantic coast from observations made by biologists and fishermen. Apparently no menhaden remain in offshore waters north of Chesapeake Bay during the colder months of the year. Hildebrand and Schroeder (1928) found that menhaden

remained in the deeper parts of Chesapeake Bay during the winter in reduced numbers, where they were taken in beam trawls; in March the fish came into shallow waters and were then taken in pound nets and haul seines. The large schools migrating up and down the coast did not enter the Bay and the local fishery was not affected by spring, summer and fall "runs" as was the case with the outer shore areas of the Atlantic States.

According to Bigelow and Schroeder (1953) menhaden left the Maine coast by the middle of October and Massachusetts Bay by early November, although small ones had been taken there as late as December. Reports from fishermen indicated that the fish went around Cape Cod to the New York region and on southward. Ellison (1951) wrote that the migrating schools were fished from Delaware south to North Carolina as follows:

"About October 15 a run of fish appears in North Carolina from the north and is joined by fish from the southern sounds and estuaries. These fish run from 10 to 12 inches in length and are known locally as 'Chesapeake Bay' fish, 'holy jumpers' or 'forerunners.' They contribute to the fishery about a month and are followed about November 10 by the so-called 'Delaware' fish, which measure 13 to 16 inches. These fish, in turn, are succeeded about Thanksgiving by 16-to-20 inch fish recognized as the 'Boston Bay' or the 'Amagansett' fish. All of the fish appearing from October 15 to November are following a north-south migration route."

In December schools of small fish 2 to 10 inches long appeared in North Carolina. Their source was unknown, but they probably came from inshore waters.

Concerning the spring migration northward Ellison said:

"The spring fishery usually starts in May, although sometimes in April. This fishery depends principally upon individuals which run from 6 to 8 inches in length and which are believed locally to come up from Florida. Usually these fish strike shoreward about the latitude of Fernandina, moving north and paralleling the coast, supplying a good fishery at Mayport, Florida. For the past four years, however, they have scarcely touched Mayport, and snapper fishermen working 30 miles out have reported great schools moving north. In these recent years they have struck first off the South Carolina coast about Georgetown and are called in North Carolina the 'Georgetown-flats' fish. These fish support the fishery in North Carolina until August, when they disappear."

Ellison further stated that the fish reached the Chesapeake region in March and April, the New Jersey and New York region in April and May, and the Maine coast in May and June. These dates are much the same as those given by Goode (1879), who reviewed all available information up to that time. Goode's data included precise dates for a 20-year period from some areas of the Atlantic coast. He did not know whether fish went south in the winter or merely offshore.

Menhaden do not always go as far north as the Gulf of Maine in summer, and combined data from Bigelow and Welsh (1925) and Bigelow and Schroeder (1953) showed that between 1845 and 1950, inclusive, menhaden had been plentiful to abundant there during only 15 of 66 years reported.

It has been generally agreed that temperature governs the north and south migrations of menhaden and that menhaden do not enter waters of temperatures less than 50° F. (cf. Ellison, 1951). Goode (1879) collected temperature records along the coast and compared them with the time of appearance of the menhaden. This information led him to state that menhaden appeared after the water temperatures rose to 50° to 51° F. and preferred temperatures between 60° and 70°. Bean (1903) noted that adult menhaden in aquaria died at temperatures lower

than 50° F. Bigelow and Schroeder (1953) said their observations corroborated the idea that menhaden did not appear in the Gulf of Maine until it was several degrees above 50. Conversely, falling temperatures drove the fish southward in the fall.

Edwards (Kendall, 1910) found that young menhaden could survive cold better than their elders. Fish 2 to 5 inches long survived water temperatures of 31.5° F. Better survival of young than of older fish at low temperatures was independently observed for other fishes by S. F. Hildebrand and Gordon Gunterfollowing cold spells on the south Atlantic and Gulf coasts. The literature was documented by Gunter (1957).

In their long migration from the south Atlantic coast to New England and back, menhaden do not follow precise routes. A "run" may strike shore for many years and then suddenly change and pass as much as 50 miles offshore. Such changes in migration routes may leave established menhaden plants fishless for several years. Ellison (1951) has given examples.

June (1958) studied the variation in meristic characters of young Brevoortia tyramus to determine whether one or more populations occur in estuarine nursery areas along the Atlantic coast. Vertebrae, ventral scutes, dorsal, and left pectoral fin rays were the meristic characters selected for examination. Counts were made on almost two thousand specimens taken from 21 locations between Cape Cod and southern Georgia.

Preliminary studies indicated that mean counts do not vary with sex, length of fish over the size range (28-150 mm.) represented, or between right and left pectoral fins. Analysis of variance applied to the meristic data gave no evidence of heterogeneity between the means of successive samples taken in any locality.

At least two populations of juvenile menhaden inhabiting the estuarine waters of the Atlantic coast of the United States were indicated, one occurring north of Long Island and another south of Long Island. Intermingling occurred in the vicinity of Long Island. Difference in mean water temperature during the time of spawning and early larval development may account for the observed differences in mean meristic counts between the two areas.

June and Reintjes (1959) noted that the purse-seine fishery depended on the appearance of schools of menhaden at the surface. Fishing started in April on the Florida coast, and by June the fish ranged from northern Florida to the Gulf of Maine. In September and October the schools began to disappear from the most northerly areas, and withdrawal proceeded southward during October. In November and December vast bodies of fish supported a sizable fishery off the North Carolina coast until early January when they once more disappeared from coastal surface water.

Food and Feeding

According to Goode (1879) a number of previous workers had observed minute organisms and the presence of chlorophyll in menhaden stomachs. However, other workers he quoted, including A. E. Verrill, thought such matter was sucked up with the bottom mud. Goode called attention to the fine gill-rakers and the fish's manner of swimming with open mouth, as if straining the water.

The definitive work on feeding and food of the menhaden was done by Peck (1894). He showed how the lamellae of the gill-rakers overlap "each other in the most perfect manner" and form a fine net for sieving the food from the water. He described a fold of mucous membrane, filled with mucous, which runs along each gill arch at the base of the gill-rakers to form a channel and, presumably, acts as a groove to carry food into the gullet. Peck's statement, "Whether there are definite ciliated tracts with this function of conveying solid particles is not yet known," still holds true.

Peck's chief conclusion, which he documented by drawings of plankton in the microscope field, was that menhaden are indiscriminate feeders, and in general take in the same materials in the same proportions as they are found in the water. In the shore waters around Woods Hole, which Peck studied, these materials were predominantly dinoflagellates, diatoms and infusorians, with annelid larvae and crustaceans in lesser abundance. Peck worked mostly with inshore and smaller fish, but found that the young ate the same food as the adults.

Peck estimated the volume of water strained by an adult menhaden and arrived at a figure of 7 gallons per minute. He estimated the food material in this amount of water to be 3.4 cc.

Hildebrand and Schroeder (1928) summarized the findings of Dr. Edwin Linton who examined the alimentary contents of 44 fish in Chesapeake Bay, "and found that in most cases they consisted of sandy mud, vegetable debris (mostly algae), and some diatoms, and in a few cases they consisted principally of copepods."

The following remarks are taken from Bigelow and Schroeder (1953):

"No other Gulf of Maine fish has a filtering apparatus comparable to that of the pogy, nor has it any rival in the Gulf in its utilization of the planktonic vegetable pasture.

'... And the food eaten at a given locality parallels the general plankton content of the water, except that none of the larger animals appear in the stomachs of the fish on the one hand, nor the very smallest organisms (...) on the other."

Schroeder (Hildebrand and Schroeder, 1928) observed that feeding fish swam in circles, rising and falling, reminding him of a whirlwind.

Ellison (1951) said the "catholic and non-discriminating taste distinguishes the menhaden as strongly exceptional, if not unique, among fishes of the sea."

Enemies and Mortality

The following succinct account is quoted from Bigelow and Schroeder (1953):

"No wonder the fat oily menhaden, swimming in schools of closely ranked individuals, helpless to protect itself, is the prey of every predaceous animal. Whales and porpoises devour them in large numbers; sharks are often seen following the pogy schools; pollock, cod, silver hake, and swordfish all take their toll in the Gulf of Maine, as do weakfish south of Cape Cod. Tuna also kill great numbers. But the worst enemy of all is the bluefish, and this is true even in the Gulf of Maine during periods when both bluefish and menhaden are plentiful there. . . Not only do these pirates devour millions of menhaden every summer, but they kill far more than they eat. Besides the toll taken by these natural enemies, menhaden often strand in myriads in shoal water, either in their attempt to escape their enemies or for other reasons, to perish and pollute the air for weeks with the stench of their decaying carcasses."

Hildebrand and Schroeder (1928) said that bluefish migrate up and down the Atlantic coast following schools of menhaden and other fish upon which they feed voraciously. The abundance of menhaden governed the movement of bluefish to some extent. In 1922 young menhaden were plentiful in the lower half of Chesapeake Bay, and the commercial catch of bluefish was greater than it had been for many years.

Ellison (1951) said the menhaden is "prey to virtually all of those carnivorous fishes which inhabit the same waters."

Goode (1879) was much impressed with predation upon menhaden. He said whales and dolphins ate them by the hogshead. From the air they were

attacked by gulls and other sea birds, and the osprey. In fact Goode mentioned every predator listed in later accounts, including gars and catfish in southern waters. He gave varied accounts of attacks by bluefish, and said the menhaden when pursued "often drive in great masses upon the shores." Goode thought the number destroyed by predators was many times that taken by man. The figure he gave, 3,000 million of millions, equals 3 quadrillion and is certainly a vast overestimate.

Ellison (1951) mentioned that bluefish sometimes ran menhaden into the
shallows in such numbers that they died
and piled up in windrows 2 feet deep,
and polluted the air. Reports of this
phenomenon extended from Hatteras
to Maine. Local health boards were
sometimes required to dispose of the
rotting fish. According to Bigelow and
Schroeder (1953) dead fish drifted
ashore along Massachusetts Bay in 1946
and 1947, and the local health boards
had to clean the beaches. However, this
kill was attributed to netting by lobster
bait fishermen.

Westman and Nigrelli (1955) made the following statement concerning annual kills of menhaden in New York:

"Menhaden appear in the New York bight in commercial quantities during late March or April and, according to reports received, the large fish precede the smaller fish by several weeks. During the latter part of May, or early June, great quantities of menhaden die in these waters and in the waters of western Long Island Sound and litter the beaches in untold numbers. Consequently, various agencies call other agencies each year, or write letters, about this phenomenon. These agencies, in turn, communicate with other agencies which, in turn, may refer the problem back to the first agency, and so on."

Dying fish were called "spinners". They were characterized by uncoordinated movements and exopthalmia. Westman and Nigrelli found hemorrhages caused by gas emboli in capillaries of the gills, eyes and optic lobes of the brain. Bacteria could not be found and the fish entrails were not harmful to cats. Whether the gas emboli were the terminal cause of death or were only an associated condition could not be determined. In any case, fish not in distress did not have gas emboli. The authors noted that all mortalities occurred in areas with "markedly varying salinities" and with "organic pollution to a degree where shellfishing is prohibited".

Parasites and Diseases

Viral and bacterial diseases are unknown in menhaden, and there is no evidence that they are affected by any fatal disease of epidemic proportions. On the other hand menhaden are characteristically host to a number of worm and crustacean parasites, which may cause debility but not death.

The following parasites of the Atlantic menhaden were listed by Westman and Nigrelli (1955):

Parasite	Structure attacked
Myxosporidian sporozoan: Chloromyxum clupeidae	Flesh.
Coccidean sporozoan: Eimeria brevoortiae (MS. name)	Male gonads. (Ellison, 1951)
Monogenetic trematodes: Diclodophora sp	Gills.
Digenetic trematodes: Hemiurus appendiculatus Podocotyl atomon Cryptocotyle lingua	Stomach. Intestine. Metacercarial cysts in skin.
Trypaborhynchid cestodes: Pterobothrium heteracanthus Rhynchobothrium sp	Cysts in viscera. Do.
Nematodes	Several ascaroids in intestine and encysted in mesentery.
Copepods: Bomolochus teres Caligus schistonyx Caligus chelifer Lernanthropus brevoortiae Lernaeenicus radiatus Clavellisa spinosa	Gills. Body surface. Do. Gills. Body surface. Gills.

Olencira praegustator, a parasitic isopod from the mouth, was not listed by Westman and Nigrelli, but is very common in fish in the south (Ellison, 1951). O. praegustator is so characteristic that its description by Latrobe, along with the original description of B. tyrannus, was one fact indicating the identity of Latrobe's fish, according to Hildebrand (1948).

Menhaden Fishery Investigations

Goode (1879) wrote of the conflicts between the menhaden fishery and other fisheries. Smith (1896) reported the first examination of other fishes taken with menhaden. Among almost 28,000,000 menhaden, the other fishes constituted 0.028 percent, exclusive of alewives. Including alewives, the figure

was 0.336 percent. Most of the clupeids other than menhaden were taken in a few sets when mistaken for schools of menhaden.

Smith also noted that "the menhaden is a fish which, as a rule, is found in comparatively close proximity to the land..." Most of the fish were taken less than 5 miles from shore.

The chief predators were found to be bluefish, sharks and weakfish. Migratory movements were often modified by the presence of "such predaceous species as bluefish, squeteague, and sharks" (Smith, 1896). The autumnal migratory movement began with the fish on the shores of Maine and Massachusetts and continued southward.

Larger and fatter fish were taken on the New England coast than from areas to the south. New England fish produced more oil in the fall than those from the same area produced in the spring. Examination of ovaries tended to verify the existence of different spawning periods on different parts of the coast.

GULF OF MEXICO MENHADEN

Spawning

Kuntz and Radcliffe (1918) noted that the first menhaden larva identified was a specimen 24 mm. long taken on January 15, 1913 by W. W. Welsh in St. George Sound, Carabelle, Florida. St. George Sound is on the northwest Florida coast and the specimen was doubtless B, patronus.

Gunter (1945) reported eight Brevoortia patronus 28-59 mm. total length taken on the Gulf beach of Mustang Island, Texas in March and April. Several larvae, tentatively identified as Brevoortia, taken at the same time, were presumed to be B. patronus.

Baldauf (1954) listed menhaden as being one of the fishes which are to be found in the lower Neches River only "during growth stages". Menhaden were taken in the Neches River at a station approximately 30 nautical miles upstream from Texas Point, at the Sabine Pass entrance to the Gulf. Salinities at stations where menhaden were taken ranged from 0.16 to 20.4%. Surface temperature varied from 14.4° to 31° C. Over 10,000 specimens were taken in 1951, 1952 and 1953. The largest menhaden measured was a specimen, found dead on the river bank, with a standard length of 150 mm. The larger fish were B. patronus but specific identification of young individuals was uncertain. Table 5 gives Baldauf's measurements.

Baldauf noted that two incoming populations, November-December and March-April, were not the same and that there may have been two spawning peaks.

Table 5.--Numbers and sizes of small menhaden taken in the Neches River, 1952-53

[Based on Baldauf, 1954]					
Date	Number	Ranges (standard length)	Mean		
July-Aug	6	40.5-93.0 mm.	58.5		
SeptOct	69	16.0-22.0 mm.	19.5		
Dec	29	19.0-23.0 mm.	21.0		
Jan	4	21.0-25.0 mm.	22.3		
Feb	14	22.0-26.0 mm.	23.1		
Mar	322	20.5-38.5 mm.	21.98		
Apr	307	18.0-40.0 mm.	21.59		

Reid (1955a) carried on an intensive study of East Galveston Bay, Texas from June 1 to July 9, 1954. Young B. patronus were abundant in the bay, and almost 21 percent of seine collections from the shallow shore zones and about 2 percent of the trawl collections were this species. Adults were uncommon in the bay. No Brevoortia were caught in six strikes with a trammel net. Little menhaden, ranging "in size from 27 to 114 mm., with most of the fish between 27 and 60 mm." (Reid, 1955b) ranked second in number in minnow seine catches and sixth in trawls.

In 20 of 30 trawl hauls, 349 B. patronus were caught (Reid, 1955b). In 10 of 14 seining operations, 1,539 menhaden were captured. Most fish were taken in the low-salinity part of the bay, at 4-12‰. Some were taken in plankton tows. Reid (1955a) suggested that the menhaden is a fish spawning offshore, and that the young come in for only a period of time.

Reid (1956) found that the percentage of menhaden greatly increased in trawl catches in East Bay after a pass to the Gulf was cut at Rollover, but greatly decreased in seine catches. The trawl catch percentage for the 2 years was 1.8 and 11.8; for the seine it was 20.7 and 1, respectively. The greatest number of menhaden were taken in the upper bays. The size range was 21 to 141 mm. standard length, with the greatest number lying between 28 and 64 mm. The collections were made in June 1955.

Reid (1957) reported further studies of East Bay, Texas, made in

1956 following the closure of the pass at Rollover. He concluded in general that physical characteristics and fauna of the bay had reverted to the 1954 state, before the pass was opened. However, "the staggering number of menhaden in the littoral zone during the 1956 study is not explained." Trawl hauls were comparable to previous years, yielding 1,000 menhaden, but 63,000 were taken in seines. The same stations were occupied as in previous years with additional hauls being made in June. The fish ranged from 18 to 60 mm. standard length with a mode at 38 mm.

Gunter (1956a) reported on larval and postlarval *B. patronus* taken in White and Grand Lakes, tributary to Vermilion Bay in Louisiana. Table 6 shows salinity ranges at which menhaden were caught. These fish were around linchlong. The length frequency data were lost. The menhaden considered in Gunter's paper were nearly all taken in minnow seines on shore and approximately 1,800 of them were taken in February 1952 and January 1953 (Gunter and Shell, 1958).

Suttkus (1956) said the movement of larvae of *B. patronus*, 20 to 30 mm. standard length, into Lake Pontchartrain started in December in 1953 and 1954 and continued into March. He assumed that spawning began in October and ceased in February. The text indicates that young fish of the year generally left the area in August to October, but according to tables presented in the paper this was not the case in 1954.

At the time Gunter (1945) worked in Copano and Aransas Bays, what he

Table 6.--The salinity ranges where small Brevoortia patronus were caught in Grande and White Lakes in Louisiana

Salinity(%)	Number	Number	Average
	caught	hauls	per haul
U.18-0.29	10	8	1.3
	1,038	15	69.2
	1,175	13	90.4

called Brevoortia sp., later named gunteri by Hildebrand (1948), was the most abundant menhaden in the bays. Of 1,231 menhaden caught, 66 percent were taken in Copano Bay and the remainder in Aransas Bay, with one batch, probably of the same species, taken on the Gulf beach. Fish largely left Copano Bay in midwinter and went into Aransas Bay. One male and one female, with running milt and eggs, were taken in the bays in February and March. The salinities and temperatures where these two fish were caught were 12.8 and 13.1% and 10.5° and $14.0\,^{\circ}$ C., respectively. The salinity range at which this species was taken was 2.0-33.7. The temperature range was 9.10-31.00 C. Postlarvae thought to be B. gunteri (as later designated) 21-30 mm. total length appeared in Copano Bay in February 1942. They were most abundant in April and could be followed until May when they were 25-45 mm. total length. A few appeared in upper Aransas Bay in April and May. All individuals in a school were near the same size. Fish more than 300 mm. in length were taken only in June, October and February. The greatest abundance was in April and May. The larger fish were most abundant in the lower bay. Smaller fish were taken in Copano Bay from February to August, in Aransas Bay only in April and May. Larger fish were in general found in the higher salinities. The impression was gained that the spawning season was in late winter and spring.

Simmons (1957), referring to the Laguna Madre of Texas, said: "Menhaden, particularly Brevoortia gunteri, were common in waters of moderate salinity and present in waters of high salinity. Menhaden definitely spawned in the area in February 1956. Individuals from 15 mm. up were taken in March, April and May." Both B. gunteri and B. patronus were listed among animals commonly taken at salinities from 20 to 60 but rarely above.

Springer and Woodburn (1960) reported on *B. patronus* taken in the Tampa Bay, Florida, area in 1958. One specimen, 22.2 mm. standard length was collected in February. In March, 569

specimens ranged from 20.1 to 31.0 mm. standard length, with the average size, 23.5 mm., coinciding with the midclass of the modal frequency. An average standard length of 27.0 mm. was recorded for 400 specimens, 17.5 to 47.5 mm. standard length measured in April. Standard length of May specimens ranged from 23.5 to 74.5 mm. with an average of 29.1 mm. All collections from February through May were from Cross Bayou Canal between Old Tampa Bay and Boca Ciega Bay where salinities ranged from 6.6 to 18.7‰ and temperatures were 20.5° to 27.5° C. During July, a series of specimens, average standard length 85.1 mm, were taken at Johns Pass, a cut between Boca Ciega Bay and the Gulf.

Springer and Woodburn reported B. smithi and B. patronus were taken together in May. The average size of B. smithi, 23.3 mm., in May was about the same as that of B. patronus in March. Additional specimens of B. smithi were reported for the months of January, June, July and August in salinity and temperature ranges of fresh water to 31.6% and 18.0-30.3°C. Young menhaden were seen at a Gulf beach station in March.

Springer and Woodburn (1960) indicated a winter spawning period for *B. patronus* and a somewhat later, spring spawning period for *B. smithi*.

Growth

Gunter (1938b), in an analysis of species taken in shrimp trawls in Barataria Bay, Louisiana, and adjacent Gulf waters, wrote that B. patronus ". . . was caught much more in the bay than outside waters. Individuals from inside were mostly immature and it is possible that adults were present in larger numbers in the Gulf. During the months of June and July in 1932 and June 1933 the menhaden was scarce inside and was taken more commonly in the Gulf. In 1932 there was a peak in the bay in January. The following year the peak came in December and January and in 1934 it came in January and February. This is ample data to

establish the fact that there is an abundance peak for this fish in the bay during the winter, which is characteristic of the life history of the species... The increased numbers caught in midwinter... are possibly a result of migration of such individuals from nursery grounds near the shore to the open bay. They grow rapidly and probably by midsummer most of them pass to the outside as the curve indicates. Fish taken on the outside were usually adult or nearly adult in size. Smaller individuals were sometimes caught near the shore."

Baldauf (1954) presented monthly standard length frequency curves for Brevoortia sp. for November 1952 through April 1953. The November mode was about 19 mm. and could be followed to a mode of 25-26 mm. in March.

Suttkus (1956) gave numerous proportional measurements of young B. patronus. These show that the body shape changes greatly between 20 and 30 mm. standard length. The meristic counts fell in the lower ranges of Hildebrand's (1948) figures. Suttkus said serrations on the ventral part of the maxillary, which disappear with age, were not mentioned by Kuntz and Radcliffe (1918) or Hildebrand (1948). However, Hildebrand called "teeth", said they were present in all species of Brevoortia, and disappeared at about 70 mm. length.

Renfro (1958)¹ took five *B. patronus* in the Aransas River, Texas, in March and July 1957. One, in March, was 120 mm. long and was in a salinity of 54.3‰. Another, 32 mm., was taken at a salinity of 47.6. Three others, 52-64 mm. long, were taken in July at 0.5‰ salinity.

Gunter (1945) in a discussion of *Brevoortia* sp. (*B. gunteri* Hildebrand, 1948) taken in Aransas and Copano Bays, Texas, said:

"Combined total length-frequency curves for both bays were made. In April, 1941 the only group of menhaden caught were from 88 to 133 mm. long with a mode at 113 and 118 mm. This group persisted until October when it was from 128 to 173 mm. long. In August a second group from 88 to 103 mm. long appeared, which became predominant in November and December. Remnants of the two groups persisted through the winter until May when they became more numerous again. At that time, the smaller group had a mode at 128 to 133 mm. Post-larvae came into the catch in January and they were predominant from then until May, when their size ranged from 23 to 43 mm. in length."

Springer and Woodburn (1960) compared data from collections in the Tampa Bay, Florida, area with Suttkus' (1956) Lake Pontchartrain data and stated that B. patronus reached Tampa Bay inland waters... 'at a smaller size (earlier age?) than it does on the Louisiana coast." It should be noted that Springer and Woodburn's collections were made close to high salinity Gulf waters while the inland waters of Lake Pontchartrain are many miles from the open Gulf and high salinity waters where spawning takes place. The data from both areas indicated "...a sudden spurt of growth after May (after June?)" by the difference between the average size of July samples. The growth rate of Florida fish seemed to be slower than fish from Louisiana.

Distribution and Migrations

According to Goode and Bean (1879) the first menhaden from the Gulf received by the U. S. National Museum were collected in West Florida in 1864. Goode (1879) under the heading of "Limits in 1877" quoted two lighthouse keepers, along the Mississippi and Texas coasts, one of whom was a former Maine pogy fisherman, who said that no menhaden "is found in those waters." However, he quoted a

¹Renfro, W. C. 1958. The effect of salinity on the distribution of fishes in the Aransas River. Master's Thesis. Graduate School, The University of Texas. 51 p., 3 tables, 25 figs.

pilot, Capt. Wm. Nichols, who said that the waters of Matagorda Bay and the Gulf were full of them and great quantities of menhaden 'drifted upon the beach at Saluria' (Texas) in 1872. Whether the fish were alive or dead at the time they stranded is not clear from the context. In the meantime Goode (1878) described Brevoortia patronus, based upon specimens from Brazos Santiago, Texas, and the mouth of the Rio Grande. Brazos Santiago remains the southernmost record for B. patronus in the western Gulf.

Jordan and Gilbert (1883) listed the menhaden from Pensacola and Galveston. Evermann and Kendall (1894) reviewed previous Texas literature and noted one young specimen from Galveston. Weymouth (1911) listed ten adults and a "considerable number" of young, the latter being doubtfully referred to Brevoortia tyrannus patronus Goode. Most of the collection was made at Calcasieu Pass, Louisiana, which lies in the range of B. gunteri, and Weymouth's doubts may have been well founded. Precise dates of collection were not given, and they were probably not known to Weymouth. The fishes were taken by Milo Spaulding during 1906.

Fowler (1931) said that a fishing vessel at Port Isabel, Texas, had a small load of *B. patronus* in August.

Gowanloch (1932, 1933), writing about the fishes of Louisiana, noted the abundance of menhaden and said that it "is not commercially fished along the Gulf Coast."

In 1932 Gunter began counting the fishes taken by the vessel "Black Mallard" in Louisiana. Five ottertrawl hauls were made monthly from the head of Barataria Bay, to 5 miles offshore from Barataria Pass in the open Gulf. Counts were made from January 1932 to June 1933; John C. Pearson continued them until December 1933. The first results were presented in a paper on destruction of fishes by shrimp trawls (Gunter, 1936). The tables were unwisely divided into commercial and noncommercial fishes and table 7 is reworked from tables Ia, Ib, IIa and IIb of that paper. Menhaden formed 5.8 percent of the 80,093 fishes taken in the bay during both years and 2.4 percent of the 46,518 fishes taken in the shallow Gulf. Most of the bay menhaden were small, and probably were able to escape the trawl when they moved out into the Gulf as larger fish.

Table 7.--Numbers of fishes taken in trawls on the Louisiana coast, 1932-33

[As reported by Gunter (1936)]

	In Bay	In Gulf	Total
Edible fishes: 1932	17,309	26,264	43,573
	24,917	11,603	36,529
Nonedible fishes: Menhaden: 1932	2,166	130	2,296
	1,767	352	2,119
Other nonedible fishes: 1932 1933	12,637	8,626	21,263
	13,465	11,790	25,255
Total nonedible fishes: 1932 1933	14,803	8,756	23,559
	15,232	12,142	27,374

Gunter (1938a) gave a further report on the data collected aboard the "Black Mallard", including collections made in 1934. Brevoortia patronus was the third ranked fish, taken in the bays, and fourteenth in the Gulf. It made up 14.1 percent of the 144,000 fishes caught.

On the basis of collections, general observations, and evidence from mass mortalities, Gunter (1941b) ranked the menhaden as second 'in species mass' among fishes in shallow waters of the northern Gulf, preceded by Anchoa mitchilli and followed by Mugil cephalus.

Gunter (1945) showed that Brevoortia ranked twelfth among all species caught in Copano and Aransas Bays and off the Gulf beach of Mustang Island, Texas; it ranked ninth in the bay catches. A comparison of trawl catches in Louisiana bays and Texas bays showed that Brevoortia ranked third in Louisiana catches and seventh in Texas. It seemed to be less common in Texas.

Fowler (1945) listed *B. patronus* from Louisiana and Galveston.

Jurgens and Hubbs (1953) included B. gunteri as one of the fishes found in the fresh waters of Texas. Knapp (1953) listed B. gunteri as ascending and B. patronus as possibly ascending Texas rivers.

H. H. Hildebrand (1953) said menhaden are not often taken in trawls by shrimpers, but sometimes large schools are encountered which burst the trawls. He reported fifteen specimens of *B. patromus* taken in two trawl hauls at 17 and 18 fathoms off south Texas.

Reid (1955a), working in East Bay, Texas, noted that where "considerable" water depth and mud bottom extended to the marsh edge, menhaden and various croakers were more abundant while atherinids and cyprinodontids were less. While sampling the Gulf beach at Gilchrist, Texas, across from East Bay, Reid (1955b) found that more

menhaden were taken than all other fishes. The 2,664 *B. patronus* caught made up 58.7 percent of the catch. Their size range was 89 to 198 mm. standard length but only nine were smaller than the largest bay fish.

Breuer (1957) said that Brevoortia sp. were not common in the high-salinity Baffin and Alazan Bays of Texas, but that a few large ones appeared in the fall and some small ones in the summer. Temperature and salinity ranges were not given for species reported in Breuer's paper.

Gunter (1950) recorded 95 specimens of B. gunteri taken along the Blackjack Peninsula shore (Aransas National Wildlife Refuge) of Mesquite and Ayres Bays, Texas from February to June 1945, where they were the third most abundant fish in minnow seines. The average monthly temperatures ranged from 19.00 to 32.10 C. and salinity range was 9.5-18.3%. In the connecting salt-flat ponds, only a few miles away, this species was taken only 8 times among 1,324 fishes, and ranked ninth in numbers caught. The average temperatures in that area during the same period were 19.0°-32.1° C. and the salinities were 4.4-12.2%.

Caldwell (1954) listed *B. gunteri* from a salt-marsh pond on Way Key, (Cedar Keys) Florida. Suttkus (1958) said the fish was *B. smithi*.

Rounsefell (1954) said that several species, including "... the menhaden, Brevoortia..." were "more or less independent of the waters between the mainland and the barrier islands."

H. H. Hildebrand (1955) reported eight specimens of *B. gunteri* from two trawl hauls in 7-8 fathoms of water off Punta Morros in the SE portion of the Gulf of Campeche. They were taken February 15, 1951. This is the southernmost record for menhaden in the Gulf. Hildebrand said he had never heard of menhaden schools south of the Rio Grande.

Gunter (1956b) recorded B. smithi, B. gunteri and B. patronus as being euryhaline.

Hubbs (1957) in a revision of a former checklist included *Brevoortia* gunteri among fishes to be found in fresh waters of Texas.

Briggs (1958) listed *B. smithi* and *B. tyrannus* from the Atlantic coast of Florida and said *B. tyrannus* was to be found on both sides of the Atlantic. He listed *B. patronus* from Tampa northward and *B. gunteri* from Cedar Keys (probably on Caldwell's record) to Campeche.

Suttkus (1958) discussed the distribution of three species of menhaden in the Gulf. In summary he said:

"The two fine-scaled species, Brevoortia gunteri and B. smithi, occur in the western and eastern Gulf respectively. The single large-scaled form, B. patronus, overlaps B. gunteri in the western Gulf from Brazos Santiago, Texas, to Grand Isle, Louisiana, and overlaps B. smithi in the eastern Gulf at Cedar Keys."

Springer and Woodburn (1960) found young B. patronus and young B. smithi together in the Tampa Bay, Florida, area. Concerning the movement of young B. patronus they said:

"In contrast to Suttkus' finding that emigration from estuarine waters took place in July and August, we found no specimens in the bay ou after May... The collection from Johns Pass...during July does indicate that migration to the Gulf had occurred at least this early and possibly as early as June."

Food and Feeding

Gowanloch (1933), Gunter (1945) and Reid (1955a) stated that Gulf Bre-voortia are plankton feeders. Darnell (1958) examined the stomach contents of 17 specimens of B. patronus from Lake Pontchartrain, Louisiana. All

contained food material. Food of small menhaden (38-48 mm.) consisted chiefly of phytoplankton with small amounts of zooplankton and plant fragments. Several species of *Anabaena* comprised 77 percent of the total food while the remaining phytoplankton was composed of diatoms. Detritus constituted 11 percent of the stomach contents. The small menhaden had obviously been straining plankton at the surface and apparently at depths below the surface.

The larger menhaden (85-103 mm.) examined by Darnell (1958) contained, in the muscular pyloric region of the stomach, 99 percent ground organic matter and silt with a few diatoms, foramniferans and copepods. Suspensions of ground up organic matter were observed, particularly along the south shore of the lake "where wave action was reducing the organic material of the marshy shore to the consistency of coffee grounds." Darnell concluded that menhaden fed by filtration, and that suspended bacteria and material other than living plankton were an important component of the food of menhaden in turbid estuaries.

Enemies and Mortality

Arthur (1931) commented on menhaden as food of the brown pelican in the following words:

"The pelican is a fish eater. While it may be true that the pelican, once in a while, may catch what man terms a 'food fish', the number of such fish of commercial value it consumes does not justify the prejudice felt against the big bird. When the World \overline{W} ar was on and the Food Administration was calling on the people to 'eat more fish', some fishermen, residents of Florida, asked that an edict be issued calling for the pelican's extermination on the theory that it was to blame for a food-fish shortage. But before this wholesale slaughter was ordered, cooler heads counseled inquiry and in the summer of 1918 the Department of Conservation conducted a

survey of the Brown Pelican breeding places, and secured exact data as to what this particular pelican ate, when fish of all kinds were most plentiful in the Gulf waters.

"The Louisiana coast from Pearl River to the Sabine was explored and pelicans and their food collected and sent to Washington, D. C. for identification by the United States Bureau of Fisheries. The result of the examination of many hundreds of stomachs showed that 97 per cent of the fish were menhaden or 'gulf sardines', and 3 per cent were silversides - not a single food fish used by man was found!"

Lund (1936) reported that about 85 percent of the dead fish reported on the south Texas coast in the summer of 1935 were menhaden. Facts reported by Lund and others verbally to the senior author indicate, with little doubt, that this mortality was the result of a "red tide".

Gunter (1941a) noted that, although menhaden were listed as a common bay fish in previous papers, only three were observed killed by the hard cold wave of January 1940 on the Texas coast. These were seen in Copano Bay and were listed as *B. patronus*. The specimens could have been *B. gunteri*.

Gunter (1945) found no menhaden in the stomachs of 237 redfish (Sciaenops ocellata) examined. He found three Brevoortia in the stomachs of 153 Cynoscion nebulosus.

Gunter, Davis, Williams and Smith (1948) recorded ten *B. patronus* killed by the red tide along 20 yards of Fort Myers beach, among 208 other fishes. The species could have been *B. smithi*.

Reid (1955a) found that 89 percent of "white trout" (Cynoscion arenarius) stomachs contained fish "and menhaden constituted the greatest part of this item." He indicated that the menhaden soon grow too large to be taken by "trout". He said menhaden were also preyed upon to a lesser extent by the croaker, two marine catfishes, the ten-

pounder, Elops saurus, and the lizardfish, Synodus foetens. It was concluded that predation on young fish, especially menhaden, is severe. Reid (1955b) also pointed out that "birds of the area also exact a toll on these fish."

Parasites and Diseases

Pearse (1952a) described the parasitic copepod, Caligus ventrosetus, from the gills of B. gunteri at Port Aransas, Texas. He also listed Lernanthropus brevoortiae from B. patronus at the same locality. Pearse (1952b) recorded Lernanthropus brevoortiae from the gills of B. patronus in Florida. Causey (1953) reported Lernaeenicus radiatus from B. "tyrannus" at Grand Isle, Louisiana.

Causey (1955) reported the parasitic copepods, Lernanthropus brevoortiae and L. radiatus from B. patronus
at Pascagoula, Mississippi. Hargis
(1955) listed the monogenetic trematode, Mazocraeoides georgei, from the
gills of B. patronus at Alligator Harbor,
Florida, as a new host record. Koratha
(1955) described a new monogenetic
trematode, Diclidophora lintoni, from
the gills of B. gunteri taken at Port
Aransas, Texas.

Hargis (1957) listed the following monogenetic trematodes (Family Mazocraeidae) as parasitic on Brevoortia patronus: Clupeocotyle brevoortia, C. megaconfibula, Kuhnia brevoortia and Mazocraeoides georgei.

Sparks (1958) listed the digenetic trematode, *Parahemiurus merus*, from the gills of *B. patronus* as a new host record.

Menhaden Fishery Investigations

Miles and Simmons (1950) gave a review of the menhaden industry and fishery. They also summarized certain biological information collected by a series of workers at the Marine Laboratory of the Texas Game and Fish Commission and published a series of mimeographed reports by Breuer,

Anderson, Knapp, Wilson, and Miles and Simmons. Miles and Simmons give the following information:

1. Other sports and commercial fishes were taken in very small quantities with menhaden. As the result of one study the figure given was one animal to 4,490 menhaden or 0.024 percent, including shrimp and crabs. The fishes caught with 5,326,000 menhaden were 36 gafftopsails (Bagre marina), 75 crabs, 91 jacks (Caranx hippos), 103 croakers (Micropogon unshrimp, 205 Spanish dulatus), 191 mackerel (Scomberomorus maculatus), 242 sand trout (Cynoscion), 304 bluefish (Pomatomus saltatrix), and a few others, all less than 8 each. The total was 7.589 other fishes.

Another study showed that 2,183 other animals, including shrimp, crabs and squid were taken with 2,500,000 menhaden.

- 2. Mackerel were found with smaller menhaden and bluefish were found with larger menhaden in offshore waters. Bluefish appeared when the smaller menhaden were replaced by larger ones in July. Crabs, shrimp, sand trout and croakers were usually taken in shallow waters. Bluefish, mackerel, tarpon, jacks and sharks seemed to be the main predators on menhaden.
- 3. Forty species of fish, comprising 26,005 individuals were examined for stomach contents. Of these, 13,288 were sea trout, Cynoscion nebulosus 3,428 were Spanish mackerel and 3,137 were redfish, Sciaenops ocellata. The remainder were 38 other species of fishes. They contained 581 menhaden. The percentages eaten by the common fishes were given. Menhaden were not preferred food of the common sports and commercial fishes.
- 4. Knapp showed that the stomachs of menhaden, mullets and "shad", remaining intact in the stomachs of predators after other parts had been digested, could be identified by their shape.

Knapp (1950) presented some of the same data and came to similar conclusions.

Filipich (1947) made five unannounced checks of menhaden boat unloadings at Mississippi factories. In 295 tons of menhaden unloaded, one mackerel and 6 white trout were found.

Gowanloch (1949) reviewed the menhaden-sports fisherman controversy and concluded that no harm was done to sports fishes by the menhaden industry.

Christmas, Gunter and Whatley (1960) reported a study of fishes other than menhaden taken in menhaden purse seines in waters around the mouth of the Mississippi River and in Mississippi Sound during the 1958 and 1959 seasons. Samples were taken from catches which totaled nearly 2 million pounds. In numbers of fish, more than 97 percent of the sampled catch were menhaden. The other fishes observed included 62 species. Brevoortia patronus was the only menhaden found in the catch. The fishery was generally prosecuted in shallow, low-salinity waters. Seventy percent of the sampled menhaden catches were made in waters of salinities between 5 and 24 parts per thousand. Surface water temperatures at the sampled seine locations varied from 22.6° to 30.5° C. Lower temperatures were encountered at the beginning and the end of the fishing season. Fishing started in May when water temperatures rose to about 23°C. and stopped in the fall when surface waters reached approximately the same temperature again.

SUMMARY

Three of the five North American species of menhaden have been found in the Gulf of Mexico. The present distribution, based on the published record, is:

1. Brevoortia gunteri, Grand Isle, Louisiana westward and southward to the Gulf of Campeche.

- 2. Brevoortia patronus, the Tampa Bay area, Florida to Brazos Santiago, Texas.
- 3. Brevoortia smithi, Cedar Keys, Florida southward and presumably around the peninsula to the Atlantic. (R. D. Suttkus, personal communication.)

Menhaden fishing in the Gulf of Mexico is dependent on *B. patronus*, and is mostly prosecuted in Louisiana waters. Gulf landings of menhaden increased rapidly with the expansion of the fishing until 1957, when landings were only 65 percent of the 1956 catch. However, 1958 landings increased to about 80 percent of the 1956 record. Apparently the 1957 decrease was caused by factors other than depletion of the population.

All information agrees with the supposition that Atlantic menhaden spawn at sea, or at least in high salinities, and the larvae work in to shore to spend their early life, very often in low salinity or even fresh water. Apparently spawning is also governed by temperature. Comparison of surface temperatures (Bumpus, 1957) for reported months of spawning along the Atlantic coast indicates that spawning takes place in the Atlantic at about the same temperature in all localities. Thus, the spawning season is during the summer on the New England coast and in the winter off the South Atlantic States.

There are no records of spawning *B. patronus* and presumably they spawn at sea. Except for one report of tentatively identified *Brevoortia* larvae on the Gulf beach in March and April in south Texas, there are no reports of menhaden larvae on the beach. On the other hand, vast numbers of larvae and juvenile menhaden have been reported in the bay waters of Louisiana and Texas. Low-salinity waters undoubtedly serve as nursery grounds.

Brevoortia gunteri in spawning condition have been reported in Copano and upper Aransas Bays, Texas, in February and March. Spawning B_{\bullet}

gunteri have been reported from the Laguna Madre, Texas, in February.

While there may be confusion between both the larvae and the young of two species where their range overlaps, reports of *B. patronus* 16-25 mm. long extend from November to June, with minimum sizes at both ends of the period. There is some evidence of a double influx of larvae. Thus the spawning season is long, over the fall and winter and into the spring. *B. gunteri* seem to spawn in the spring in Texas waters.

Menhaden eggs and early larvae have not been reported in the Gulf. Presumably, the eggs are bouyant like those in the Atlantic and the larvae remain near the surface, as has been reported in Virginia.

The slender larvae which enter estuarine waters undergo metamorphosis between 20 and 30 mm. standard length in Lake Pontchartrain. Data on growth rates are scarce. A group thought to be *Brevoortia gunteri* ranged from 88-133 mm. long in April and 128-173 mm.long in August in Texas waters. A group of Texas *Brevoortia* 88-103 mm. long in August had a mode of 128-133 mm. the following May.

On the Atlantic coast, menhaden undertake extensive migrations up and down the coast with changes in season, during which they are followed by the fishermen, at least on the trip south. Nothing similar is known in the Gulf, probably because it is an east-west coast.

Large menhaden are not common in the bays and evidently the young fish move out, as they grow up, mostly in late summer and fall. Salinity is a critical factor in the development of larval Atlantic menhaden, with low salinity waters being essential to normal development. In Texas, larvae and juveniles 21-48 mm. long have been found at salinities of 2.0-20.4% and temperatures of 15.5°-31.0°C. In White Lake, Louisiana, menhaden larvae have been found in virtually fresh water.

The numbers of larvae found in the bays may vary enormously from year to year. There may be some connection between the heavy 1956 commercial production of menhaden and Reid's report of "staggering" numbers of larvae in East Bay, Texas, in the summer of the same year.

There is only one report on the food of Gulf menhaden. It was found that Lake Pontchartrain menhaden fed by filtration and consumed considerable quantities of detritus and suspended bacteria in addition to living plankton.

Menhaden in the Gulf of Mexico are not known to be chased ashore by predators or to die in recurring summer maladies from unknown causes as they do in the Atlantic. They have been killed in considerable numbers by the red tide in Texas and Florida but these instances are outside the commercial range. Menhaden seem to be resistant to sudden cold waves which decimate other fishes in Texas and Florida, and none were reported killed in three studies of cold-killed fishes in Florida and Texas. A few menhaden have been reported killed by the cold on the Texas coast.

Menhaden fishermen on the Gulf catch few other fish, comparable to the situation on the Atlantic coast. The chief menhaden enemies seem to be bluefish, mackerel, sharks, and tarpon. The common shore and shallowwater sports and commercial fishes seem not to subsist to any great extent on larger menhaden, but predation upon small menhaden in the bays seems to be very heavy.

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